The role of *Pteridium arachnoideum* (Kaulf) on the seed bank of the endangered Brazilian Cerrado

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Abstract

The native bracken *(Pteridium arachnoideum*) often occurs in mono-specific stands in the Brazilian Cerrado, and this dominance can impact on both the above-ground vegetation and soil seed bank. This study investigated how invasion by this species over a 20-year period changed the seed bank, and the relationship between the seed bank and litter mass. Soil samples were taken from three replicated invaded and uninvaded sites, and seedling emergence followed for six months. The above-ground biomass and litter of *P. arachnoideum* were collected in ten $1m^2$ plots from three invaded sites. No difference was found between invaded and uninvaded areas in seed bank richness, diversity or overall abundance. The most abundant family was the Melastomataceae, followed by the Poaceae. The Melastomataceae was more abundant in uninvaded sites, but the most common species on this family (*Tibouchina stenocarpa*) was not affected. The grasses were more common in invaded sites in the rainy season and were affected by heterogeneity in the litter layer. The seed bank could play a role in the recovery of these invaded areas, but this could be constrained by the presence of weeds and invasive grasses.

Keywords: Bracken; Melastomataceae; litter; savanna; biological invasion.

Resumo

O samambaião (*Pteridium arachnoideum*) frequentemente domina áreas de cerrado, e pode alterar tanto a vegetação estabelecida quanto o banco de sementes do solo. Nesse estudo investigamos como áreas de cerrado invadidas por essa espécie a mais de 20 anos alteraram o banco de sementes, e também a relação entre banco de sementes e quantidade de serapilheira. Extraímos amostras de solo em três invadidas e em áreas controle adjacentes, e monitoramos a emergência de plântulas por seis meses. Coletamos a biomassa aérea e a serapilheira de *P. arachnoideum* em dez parcelas de $1m^2$ nas áreas invadidas. A riqueza, diversidade e abundância total não diferiram entre áreas invadidas e controle. A família mais abundante foi Melastomataceae, seguida por Poaceae. Melastomataceae foi mais comum em áreas controle, mas não a espécie mais comum nessa família (*Tibouchina stenocarpa*). Gramíneas foram predominantes em áreas invadidas durante a estação chuvosa, e foram afetadas pela heterogeneidade da camada de serapilheira. O banco de sementes pode ser importante para a recuperação dessas áreas invadidas, mas esse uso pode ser prejudicado pela presença de ervas daninhas e gramíneas invasoras.

Palavras-chave: samambaião; Melastomataceae; serapilheira; savana; invasão biológica.

Introduction

Invasive species often form mono-specific stands that impact on native plant communities (Pivello et al. 1999). These invasive species can outcompete established native species, reducing both their number and abundance, and altering the structure and function of the invaded communities (Marchante et al. 2011). As a consequence, the restoration potential of the ecosystem is affected, especially in areas where dispersal from nearby seed sources is limited (Funk et al. 2008). In addition, many invasive species have also been shown to impact negatively on the soil seed bank (Pakeman and Hay 1996; Gioria et al. 2012). Therefore, even if the invasive species were to be reduced through either a natural decline or deliberate weed control, it is expected that at least some native species will have difficulties in re-establishing because of the reduced number of viable seeds in the soil (Wearne and Morgan 2006). The worst case scenario is where there is a reduction in native species seeds/propagules and an increase in the invading species seeds/propagules in the soil seed bank (van der Valk and Pederson 1989).

Invasive species can contribute to the impoverishment of seed banks in three ways: first, by decreasing the local seed rain by outcompeting established individuals of native species, thus fewer seeds of these species will be available to be incorporated (Gioria et al. 2014); second, by interfering with seed transfer to the soil by producing a very thick litter layer (Ghorbani et al. 2006), and third by increasing the number of its own propagules (Gioria et al. 2012). Consequently, we could expect an increasing impoverishment of the native soil seed bank where invasive species have colonized and persisted for a long time. The degree of impact, therefore, will depend on the abundance of the invasive species and on the length of time since invasion (Gioria et al. 2014). In spite of the growing interest on the impact of biological invasions, relatively few studies have assessed the impacts of invasive species on the seed bank (Wearne and Morgan 2006; Gioria and Osborne 2010; Gioria et al. 2014), and

especially in neotropical regions (Silva and Silva Matos 2006; Herrera and Nassar 2009). Knowledge of the native species propagules and seeds remaining in the soil bank is an essential pre-requisite for the successful implementation of restoration programs in affected areas. Here, we investigate the effect of the invasion-dominance by the native fern species *Pteridium arachnoideum* (Kauf) Maxon (Dennstaedtiaceae) on soil seed banks in Brazilian Cerrado.

Brazilian Cerrado, a shrub-covered savanna, is considered one of the 25 most endangered ecosystems in world because of its high biodiversity and high level of destruction (Myers et al. 2000). In South America, it formerly covered about 2 million km^2, mostly in the Brazilian Central Plateau (Gottsberger and Silberbauer-Gottsberger 2006), but in the last decades it has been reduced considerably. For example, in 1962 the total area of Cerrado in São Paulo state, Brazil covered about 33,929 km^2 (13.7%) (Borgonovi and Chiarini 1965) but 30 years later in 1992, it was reduced to 2,379 km^2 (<1%) (Kronka et al. 1998). Given that continuous loss of Cerrado, any expansion of invasive species in its remnants will increase its degradation through continuing loss of biological diversity (Pivello et al. 1999; Miatto et al. 2011). One problematic invasive species of these areas is *Pteridium arachnoideum*, which although being a native species, can be an aggressive weed species in some areas of Brazilian ecosystems (Pivello et al. 1999; Silva and Silva Matos, 2006).

In this paper we tested two main hypotheses concerning the effects of *P. arachnoideum* on the Cerrado soil seed bank: (1) *P. arachnoideum* invasion reduces the size and composition of the soil seed bank compared to uninvaded sites; (2) the deep litter layer produced by *P. arachnoideum* after invasion impacts negatively on the soil seed bank. A meta-analysis assessing the effect of invaded species on the soil seed bank found that in most cases invasion produced a negative effect on the abundance and/or richness of native species, especially in invasions by large herbaceous species (Gioria et al. 2014). We, therefore, expect

a negative effect of *P. arachnoideum* on the seed bank in the Cerrado sites, because in mono-specific stands *Pteridium* species in both temperate and tropical regions have been shown to reduce the seed bank diversity (Pakeman and Hay 1996; Mitchell et al. 1998; Silva and Silva Matos 2006). We also expect a negative relationship between litter biomass and seed bank abundance, considering that dense litter layer in *Pteridium*-dominated stands can be a barrier to seeds reaching the soil (Ghorbani et al., 2006).

Methods

We carried out this study in the Dr. Antônio T. Viana Ecological Park (21º 58' and 22º 00' S, 47º 51' and 47º 52' W; 72 ha) in São Carlos municipality, São Paulo state, Brazil. The climate has a rainy (October-March) and a dry season (April-September). The soils are latossols (Lorandi 1985) and the vegetation is either gallery forest or Cerrado *sensu stricto*, a typical savanna with a discontinuous canopy of shrub and tree species (Coutinho 1978). According to local people, *P. arachnoideum* has been found in the park since its foundation in 1984, but its expansion into the study sites occurred after a fire in 1994. We compared the seed bank in three sites which had become dominated by *P. arachnoideum* over a 20-year period to those in three adjacent areas where *P. arachnoideum* was absent. *Pteridium* is a well-known weed worldwide, but most knowledge has been derived from studies in the northern hemisphere (Marrs and Watt 2006). *Pteridium* may have a large underground rhizome network (Marrs and Watt 2006) and achieve high rate of vegetative growth (den Ouden 2000). These abilities enable the species to produce a dense frond canopy and deep litter layer, which prevents colonization by other plant species (Ghorbani et al. 2006; Silva and Silva Matos 2006). These attributes provide *Pteridium* the ability to colonize and produce essentially mono-cultures. *P. arachnoideum*, causes similar problems in South America (Alonso-Amelot and Rodulfo-Baechler 1996; Hartig and Beck 2003; Silva and Silva Matos 2006), suppressing understory species especially after fire (Silva-Matos et al. 2005)

We collected seed bank samples within each of the six sites (three invaded by *P. arachnoideum* and three uninvaded) in both the wet and the dry season to test for any seasonal differences. At each site, we located 10 1 x 1m plots randomly and collected a soil sample (23cm diameter, 5cm depth). In order to investigate the relationship between biomass production and seed bank composition, we also sampled the above-ground biomass and litter layer during the wet season from the 1 x 1 m 10 plots within the three areas invaded by *P. arachnoideum*. The wet season was sampled because *P. arachnoideum* seems to have a larger biomass production during this period (Portela et al. 2009b). The biomass was harvested at ground level and separated into three fractions: biomass, litter of *P. arachnoideum*, and litter of other species. These fractions were dried at 80 °C for 48 h and weighed.

We determined the size and composition of the soil seed bank by counting emergent seedlings under controlled conditions. This method is considered the most reliable for determining species composition of seed banks in plant communities (Roberts 1981). We spread the soil samples into 21 x 26 cm germination trays to a depth of 3.5cm (Dalling et al. 1995), and covered them with crystal clear plastic to decrease airborne contamination and maintain humidity. Trays containing soils sterilized at 80°C for 72h were distributed randomly among the germination trays to assess airborne contamination. All trays remained in a greenhouse under natural conditions of air humidity and temperature for six months. They were kept moist, and the number of emergent seedlings recorded weekly. We promptly identified seedlings to species level, and when this was not possible, we transferred them to individual pots for subsequent identification.

We analyzed individual soil seed bank variables (total species abundance, richness, Simpson's diversity index, abundance of the four most abundant plant families, abundance of five of the most common native and exotic species) with generalized-linear-mixed-models (GLMM) using the 'glmmadmb' function in the 'glmmADMB' package (Fournier et al.

2012) implemented in the R Statistical Environment (v.3.1.0 R Development Core Team, 2014). Season (wet *versus* dry) and *P. arachnoideum* invasion/no invasion were treated as a categorical fixed factors, and plots nested within site and season were included as random factors with random intercept to account for the spatial structure of the design (Pinheiro and Bates 2000). We assumed a Gaussian error structure for species diversity, and a binomial error structure for the rest of variables. There were a large number of zero data points for *Melinus minutifolia* (P. Beauv.) and *U. decumbens* Stapf, and accordingly a zero-inflated model was applied to these species (Zuur et al. 2009).

We assessed the relationship between the seed bank and the biomass and litter production in sites dominated by *P. arachnoideum* (rainy season only) using multiple linear regressions. Dependent variables were richness, overall abundance and abundance of the most common families and species in the seed bank, and independent variables included density, biomass and litter (both *P. arachnoideum* and litter from other species). This more simple analysis was adopted because GLMM analyses showed no significant random effect related to sites. We considered as best model those with lowest Bayesian Information Criterion (BIC) values. All models were performed and compared in the R Statistical Environment (R_Development_Core_Team 2014).

Results

A total of 2793 seedlings emerged during the experiment, 1531 from areas invaded by *P. arachnoideum* and 1262 from uninvaded areas. About 71% of all seedlings were identified to species level, 19% to genus level, 6% to family level and only 4% remained wholly unidentified. Seedlings belonged to 11 families and 56 species, with six species responsible for 73% of all individuals (Table 1). The most abundant family was the Melastomataceae, mainly represented by *Tibouchina stenocarpa* (DC.) Cogn. and *Leandra aurea* (Cham.) Cogn. (Table 1), followed by the Poaceae, mostly represented by the African species *Melinis*

189 *minutiflora* P. Beauv. and *Urochloa decumbens* (Stapf.) R.D. Webster. Native species from
190 the Rubiaceae and Asteraceae were common, but these were mainly small herbs and ruderal
191 species (Table 1). All other families were less abundant, often being represented by a single
192 species (Table 1).

193 The GLMM models showed a significant interaction between seasonality and the
194 presence of *Pteridium arachnoideum* in total seed abundance (Table 2a, Figure 1a), showing
195 that there was an increased abundance in control sites in the dry season compared to *P.*
196 *arachnoideum*-invaded sites (Figure1a, $p<0.05$), whereas in the wet season the differences in
197 total seed abundance between invaded and uninvaded sites disappeared (Figure1a, $p>0.05$).
198 Surprisingly, GLMM models showed no significant effect of the presence of *P.*
199 *arachnoideum* on seed bank richness and diversity (Fig 1a).

200 The abundance of Melastomataceae was significantly lower in the seed bank of invaded
201 sites, although there was no season or invasion x season interaction (Tab 2b, Fig 2a). Within
202 this family, however, *Leandra aurea* showed a lower abundance in invaded sites (Table 2c,
203 Figure 3d). The seed bank abundance of the Asteraceae and Poaceae, as well as the most
204 common species on these families, showed a significant interaction between invasion and
205 season (Table 2b). The abundance of Poaceae and *M. minutiflora*, which represented most of
206 individuals in this family, was greater in the invaded sites in the rainy season, but lower in
207 these same sites in the dry season (Table 2b,c, Figure 2b, Figure 3b). *U. decumbens* was
208 always more abundant in the invaded sites compared to the controls (Table 2c, Figure 3e). On
209 the other hand, Asteraceae and *Baccharis linearifolia*, the most abundant species in this
210 family, showed a significant invasion x season interaction (Table 2b,c, Figure 2c, Figure 3c).
211 Both were significantly more abundant in invaded sites in the rainy season, whereas in the

dry season this difference disappeared. Finally, there were no significant effects of *P. arachnoideum*-invasion and season on the abundance of the Rubiaceae (Table 2b, Figure 2d).

The linear model with the lowest BIC values to the relationship between seed bank and biomass/litter production included only the amount of litter produced by *P. arachnoideum* and other species litter as independent variables (Table 3). The abundance of Poaceae and *M minutiflora* were significantly negatively related to the amount of litter produced by *P. arachnoideum* (Table 3). Conversely, there was a positive effect of the amount of litter produced by other species on the seed bank abundance of Poaceace, total abundance, Asteraceae, Rubiaceae, *M. minutiflora* and *U. decumbens* (Table 3); the models for the total abundance (P=0.033), the Asteraceae (P=0.049) and the Rubiaceae (P=0.038) were only marginally significant (Table 3).

Discussion

Our results suggest that abundance, richness and species diversity of the soil seed bank in sites dominated by *P. arachnoideum* was similar to uninvaded sites. The absence of a negative effect of invasive species in the seed bank richness has been commonly reported, but most of these studies found at least a lower abundance of native species in invaded sites (Gioria et al. 2014). We believe that this might be related either to the dominance of a few species with more persistent seed banks in both invaded and uninvaded sites or to the relatively short time since invasion. Nevertheless here the invasion occurred over 20 years, stands in the northern hemisphere, where *P. aquilinum* (L.) Kuhn also has impacted on seed banks, have been colonized for centuries (Ghorbani et al. 2007). Negative effects of *P. arachnoideum* on the seed bank of Cerrado sites were limited to the Melastomataceae, of which only one, relatively less common native species (*L. aurea*) showed an individual significant reduction. This result contrasts previous studies, which found a lower abundance

236 or richness of native species in *Pteridium* stands (Pakeman and Hay 1996; Mitchell et al.
237 1998; Silva and Silva Matos 2006).

238 It seems that our results were also affected by the low richness of woody species in the
239 seed bank of both invaded and control sites. Both invaded- and uninvaded-sites had a lower
240 number of woody species than would be expected considering the local woody flora
241 described previously in the study area by Miatto et al (2011). Miatto et al detected 33 woody
242 species in the same invaded sites and 64 in the adjacent uninvaded sites, which in general
243 were also more diverse. Here, we only found five tree species in the seed bank of the same
244 sites (invaded 5 species, *versus* uninvaded 3 species), but a single very abundant species (*T.*
245 *stenocarpa*) was the responsible for most occurrences. These large dissimilarities between the
246 composition of the seed bank and the established vegetation were expected, because the
247 maintenance of a large seed bank is just one of many regenerative strategies adopted by
248 tropical species (Thompson and Grime 1979; Simpson 1989; Grime 2001). Many of the tree
249 species, like many tropical species, produce recalcitrant seeds, and hence they do not produce
250 a persistent seed bank (Vazquez-Yanes and Orozco-Segovia 1993). However, we believe the
251 high disparity found in here may also be related to intrinsic characteristics of the Cerrado
252 vegetation, where several species reproduces either vegetatively though a bud bank or though
253 the germination of recently-dispersed seeds, usually after disturbance (Hoffmann 1998).
254 Consequently, remarkable differences between invaded and uninvaded sites concerned to the
255 established woody vegetation (Miatto et al. 2011) could not be found in the seed bank.

256 The seed morphology of the dominant species in the seed bank of both invaded and
257 uninvaded sites highlights the prevalence of persistent seed banks in high biomass sites
258 dominated by *Pteridium*. Studies on *Pteridium aquilinum* stands on British heathlands
259 revealed that its seed bank is often dominated by *Calluna vulgaris* (L.) Hull (Ericaceae), a
260 native shrub that produces large amounts of small seeds (Pakeman and Hay 1996). In the

261 Atlantic Forest, Silva and Silva Matos (2006) observed that *Tibouchina* sp. (Melastomataceae)
262 was the second commonest genus in the seed bank of *P. arachnoideum*-dominated areas.
263 Like *C. vulgaris*, seeds of *Tibouchina*, including *T. stenocarpa*, the most common species
264 found in their study, are small and abundantly produced (Barroso et al. 1999; Pinheiro and
265 Ribeiro 2001). A review of temperate communities found a negative association between
266 seed size and persistence in the seed bank (Thompson et al. 1998). Dormancy mechanisms
267 were reported for *Tibouchina* genus (Silveira et al. 2012), and could also have contributed to
268 the presence of *T. stenocarpa* even in sites with a poor seed rain and subject to a long-term
269 presence of *P. arachnoideum*. In addition, we believe that the dominance of these small seeds
270 in invaded sites may be intensified by the dense above-ground biomass and deep litter layer
271 observed in *Pteridium* stands, which could be an effective barrier to incorporate larger seeds
272 into the soil seed bank (Ghorbani et al. 2006). This could also explain the lower abundance of
273 *L. aurea* in sites with *P. arachnoideum*, as that his species produces fleshy fruits and
274 relatively large seeds which zoocoric dispersion (Manhães 2003).
275 Even though species with small seeds and persistent seed bank are dominant in the
276 invaded sites, exotic grasses and ruderal native species seem to maintain a transient seed
277 banks in sites dominated by *P. arachnoideum*. Our results showed that *M. minutiflora* and *B.*
278 *linearifolia* were more common in the seed bank of invaded sites in the rainy season, while in
279 the dry season they were more abundant in control sites or had similar abundance regardless
280 of the invasion by *P. arachnoideum*, respectively. A similar tendency occurred to *U.*
281 *decumbens*, although it was more common in invaded sites also in the dry season. Such
282 variability is commonly found in the soil seed bank, and is frequently related to the
283 differences in the timing and scales of propagule dispersion, longevity in the soil and
284 incorporation into the seed bank (Thompson and Grime 1979; Simpson 1989). Since this
285 heterogeneity on the seed bank occurs in species with transient seed banks (Thompson and

286 Grime 1979), it seems that *M. minutiflora* and *B. linearifolia* have a less persistent seed bank
287 compared to species from Melastomataceae family.

288 Although our results showed a good performance of *P. arachnoideum* in the study sites,
289 high within-site heterogeneity may also have contributed to the absence of a clear negative
290 effect of *P. arachnoideum* even over species with transient seed banks. The mean frond
291 biomass of *P. arachnoideum* (958 ± 370 g/m^2) is greater than found in most *P. aquilinum*
292 stands (Marrs and Watt 2006), and also than that obtained for *P. arachnoideum* in both high-
293 altitude areas in Venezuela (287 ± 22.4 g/m^2) (Alonso-Amelot and Rodulfo-Baechler 1996),
294 and in the Atlantic Rain Forest (236 g/m^2) (Portela et al. 2009a). Conversely, the mean litter
295 biomass (1012 ± 285 g/m^2) was low compared to that obtained by Bray (1991) to *P.*
296 *esculetum* (G. Forst.) Cockayne (3364g/m^2), but is larger than found in the Atlantic Rain
297 Forest to *P. arachnoideum* (751 g/m^2) (Portela et al. 2009a). An increased overall above-
298 ground biomass\litter has been considered to have negative effects on local seed rain in
299 invaded sites, and therefore, an impact on soil seed banks (Gioria et al. 2012). However, it is
300 expected that some local heterogeneity in the level of invasion, mostly because suitability of
301 local abiotic conditions and time since the invasion would be highly variable. We believe that
302 within-site variation in above-ground and litter biomass in our sites, which possibly is as a
303 result of its relatively young age of the stands (20 years), may have decreased the overall
304 effect of *P. arachnoideum* on the seed bank related to control sites, altogether with the low
305 richness and the expected high spatial heterogeneity in the seed bank (Thompson and Grime
306 1979).

307 The importance of spatial heterogeneity inside *Pteridium* stands for transient seed banks
308 is highlighted by the relationship between the presence of African grasses and the litter
309 accumulation. The abundance of *M. minutiflora* in the soil seed bank was negatively
310 correlated with the amount of *P. arachnoideum* litter, but positively correlated with the

311 amount of other species litter. We believe that these responses may be related to the short-
312 term longevity *M. minutiflora* seeds in the soil. Given that seed bank presence depends on
313 effective seed rain and successful seed incorporation into the soil (Thompson and Grime
314 1979), it is hypothesized for this species that incorporation was less effective under the larger
315 amount of litter produced by *P. arachnoideum,* acting as a barrier to seed arrival into the soil
316 (Ghorbani et al. 2006). On the other hand, the presence of litter from other species was a
317 direct consequence of the presence of other species, which may have created microsites with
318 lower litter accumulation e allowed higher rates of seed incorporation into the soil (Ghorbani
319 et al. 2006). This could explain why the relationship between seed bank and litter was highly
320 significant for African grasses (*M. minutiflora* and *U. decumbens*) which have a short-term
321 seed bank, weakly significant for ruderals from the Asteraceae and Rubiaceae with a more
322 constant seed bank, and absent for the Melastomataceae with persistent seed bank.
323 Our results suggest that microsites where *P.arachnoideum*-dominance is less
324 pronounced can maintain more transient seed banks. However, in our study sites these
325 species are weeds and invasive grasses, whose regeneration could impair restoration of native
326 species from the seed bank pool. Pioneer species, e.g. the Melastomataceae, are commonly
327 found both in the seed bank and in the initial process of natural succession (Baider et al.
328 2001; Grime 2001; Silva and Silva Matos 2006). Consequently, the presence of *T. stenocarpa*
329 in the seed bank, even in stands dominated by *P. arachnoideum,* could be an important for
330 the restoration of these sites. However, the occurrence of fire and climatic seasonality can
331 limit the establishment of plants from seeds in Cerrado (Hoffmann 1998; Gottsberger and
332 Silberbauer-Gottsberger 2006), so that an effective vegetation restoration strategy reliant on
333 seed banks would depend on a large amount of native seeds in the soil. Unfortunately, the
334 remaining dominant native species in the *P. arachnoideum* - invaded areas were short-lived
335 perennials from the Asteraceae and Rubiaceae families, whose seed banks may have small

role in restoration of these sites. Similarly, the presence of exotic species as *U. decumbens* and *M. minutiflora* in the seed bank of invaded sites may be considered a negative effect of *P. arachnoideum.* The dominance of these undesirable species in the seed bank is a common consequence of long-term invasions (Gioria et al. 2012; Gioria et al. 2014), and have been reported for sites invaded by *Pteridium* (Marrs and Watt 2006, Silva and Silva Matos 2006). The presence of *U. decumbens* and *M. minutiflora*, in both the established vegetation and seed bank, appears to be an important constraint for seed regeneration of native species, given that both are highly invasive species in the Cerrado (Pivello et al. 1999; Barbosa et al. 2008; Hoffmann and Haridasan 2008). Both species are superior competitors to native grasses, achieve high growth rates under favourable conditions and often spread after fire (Williams and Baruch 2000), specially *U. decumbens* (Pivello et al. 1999). These abilities could favour these species in *P. arachnoideum*-invaded sites, with are especially subject to fire because of the large amount of dry biomass (Silva Matos et al. 2002), or in invaded sites where mechanical removal is often used as a management tool (Marrs and Watt 2006).

Our results did not support the hypothesis of an impoverished soil seed bank in sites invaded by *P. arachnoideum* over a period of 20 years. However, both life-history aspects and the high litter production of *P. arachnoideum* may constrain the soil seed bank richness and abundance in the future. The negative association between seed bank abundance and litter layer indicates that heterogeneity of the dominance of *P. arachnoideum* may give an opportunity to the development of a seed bank with more transient species. However, in our study sites these species are native weeds and African invasive grasses. The accumulation of these undesirable species might limit a seed bank centered restoration in Cerrado sites dominated by *P. arachnoideum*. This is an addition threat to this vegetation type, which in the southeast of Brazil is already highly fragmented and threatened from development and changed fire regimes (Durigan et al. 2007).

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Table 1 – Species composition and seed abundance in the soil seed bank in the three sites invaded by *Pteridium aracnoideum* (P1, P2 and P3) and in the three uninvaded sites (C1, C2 and C3) of Cerrado in the Southeast Brazil in both the rainy and dry season. Families and species within families are showed in decreasing order of total abundance in the soil seed bank. Species origin and status abbreviation: nat- native, rud-ruderal, ex-exotic, inv- invasive.

Taxa	Habit	Origin/	Rainy season						Dry season					
		status	C1	C2	C3	P1	P2	P3	C1	C2	C3	P1	P2	P3
Melastomataceae														
Tibouchina stenocarpa	tree	nat	24	43	19	4	58	46	1	8	108	2	44	176
Leandra aurea	shrub	nat	20	54	16	7	19	9	45	81	16	38	33	9
Miconia albicans	shrub	nat	9	0	3	3	1	0	15	3	0	3	0	2
Miconia rubiginosa	tree	nat	7	0	1	0	1	0	0	0	1	1	0	0
Miconia ligustroides	tree	nat	0	0	0	0	0	0	1	3	0	0	0	1
species 1			0	0	0	2	0	0	0	0	0	0	0	0
species 2			0	0	0	0	0	0	15	0	0	0	5	1
Undefined			1	0	0	0	0	0	6	7	13	3	12	2
Poaceae														
Urochloa decumbens	herb	exo/inv	1	0	7	28	5	30	0	3	0	0	5	1
Melinis minutiflora	herb	exo/inv	21	3	4	89	2	18	96	121	97	1	10	1
Panicum campestre	herb	nat	1	0	1	0	2	0	0	6	17	0	0	13
Panicum sp.	herb		5	6	0	0	0	4	1	0	0	0	0	0
Paspalum pilosum	herb	nat	0	0	1	0	0	0	0	1	0	0	0	0
Axonopus capillaris	herb	nat/	0	0	0	0	0	0	0	0	1	0	1	0
species 1	herb		0	2	0	1	0	0	0	0	0	0	0	0
Eleusine indica	herb	nat/rud	0	0	0	0	0	0	0	0	0	0	0	1
species 2	herb		0	0	0	0	0	9	0	0	0	0	0	0
Undefined			4	20	0	1	0	0	0	1	0	3	3	1
Asteraceae														
Baccharis linearifolia	shrub	nat	0	26	6	37	62	78	40	12	25	11	33	19
Mikania sp.	vine		10	4	5	11	4	11	3	2	8	8	17	4
Baccharis dracunculifolia	shrub	nat	3	0	2	0	9	6	1	15	0	0	4	1
Chromolaena sp.	shrub		1	0	8	0	0	0	0	2	4	0	1	2
species 1			1	0	0	2	0	0	0	0	0	0	0	0
species 2			0	0	0	1	1	0	0	0	0	0	0	1
Pterocaulon alopecuroides		nat/rud	0	0	0	1	0	0	0	0	0	0	0	0
Rubiaceae														
Spermacoce sp. 1	herb		76	3	1	1	17	9	57	6	0	5	5	16
Spermacace sp. 2	herb		33	2	1	3	38	15	3	24	42	2	8	14
Coccocypselum lanceolatum	herb	nat	0	0	0	0	0	0	2	0	0	0	1	0

Continuation (...)

Taxa		Origin/	Rainy season						Dry season					
		status	C1	C2	C3	P1	P2	P3	C1	C2	C3	P1	P2	P3
Cyperaceae														
Cyperus aggregatus	herb	nat/rud	0	0	0	0	0	0	7	9	13	0	4	0
Fimbristylis spp.	herb		0	0	0	0	0	0	5	0	0	0	0	26
Cyperus surinamensis	herb	nat	0	0	0	0	0	0	3	0	1	1	0	1
Undefined			1	0	7	0	2	2	2	12	10	1	0	0
Fabaceae														
species 1			0	0	0	0	0	0	0	5	0	0	0	0
Zornia latifolia	herb	nat	0	0	0	0	0	0	0	2	0	0	0	0
Chamaecrista rotundifolia	herb	nat	0	0	0	1	0	0	0	0	0	0	0	0
Senna chrysocarpa	herb	nat	0	0	0	0	0	0	0	0	0	0	1	0
Undefined			1	0	0	0	0	0	1	0	0	0	1	0
Lithraceae														
Diplusodon virgatus	shrub	nat	16	1	0	0	0	0	0	0	0	0	0	0
Cucurbitaceae														
species 1	vine		0	0	0	0	1	0	0	0	0	0	0	0
Primulaceae														
Rapanea umbellata	tree	nat	0	0	0	0	2	0	0	0	0	0	2	0
Rosaceae														
Rubus sp.	shrub		0	0	0	0	0	0	0	0	0	0	3	0
Euphorbiaceae														
Maprounea guianensis	tree	nat	0	0	0	0	0	0	0	0	0	2	0	0
Indeterminated			5	54	2	3	0	0	1	2	2	18	16	4

Table 2. Results of General Linear Mixed-Effects Models assessing the effects of *P. arachnoideum* invasion on soil seed bank composition in both the dry and rainy seasons in Cerrado *sensu stricto* vegetation in Brazil, based in different dependent variables. (a) Total abundance, richness and species diversity. (b) Total abundance and of the five major plant families, (c) abundance of the most common exotic and native species. All models assumed a negative binomial distribution, except to species diversity, where we assumed a Gaussian distribution. * denotes zero-inflated models were fitted. Significance: ns=P>0.05; * =P<0.05; **=P<0.01; ***=P<0.001. The intercept is vegetation with no *P. arachnoideum* invasion in the wet season; Pa.inv = *P. arachnoideum* invasion and Dry.S = dry season.

(a)

Variables	Factor	Estimate	SE	z	P	Significance
Total abundance	(Intercept)	2.995	0.149	20.08	<0.001	***
	Pa.inv	0.064	0.194	0.33	0.741	ns
	Dry.S	0.502	0.218	2.30	0.021	*
	Pa.inv x Dry.S	-0.626	0.269	-2.33	0.020	*
Richness	(Intercept)	1.778	0.113	15.77	<0.001	***
	Pa.inv	-0.089	0.112	-0.79	0.430	ns
	Dry.S	-0.007	0.110	-0.06	0.955	ns
	Pa.inv x Dry.S	-0.018	0.157	-0.11	0.910	ns
Simpson 1-D	(Intercept)	0.677	0.031	21.79	<0.001	***
	Pa.inv	-0.078	0.041	1.88	0.063	ns
	Dry.S	-0.047	0.049	-0.97	0.335	ns
	Pa.inv x Dry.S	0.092	0.058	1.59	0.110	ns
(b)						
Melastomataceae	(Intercept)	1.957	0.229	8.55	<0.001	***
	Pa.inv	-0.722	0.272	-2.65	0.008	**
	Dry.S	0.393	0.249	1.58	0.110	ns
	Pa.inv x Dry.S	0.575	0.355	1.62	0.105	ns
Poaceae	(Intercept)	1.035	0.288	3.60	<0.001	***
	Pa.inv	0.806	0.388	2.07	0.038	ns
	Dry.S	1.405	0.385	3.65	<0.001	***
	Pa.inv x Dry.S	-2.957	0.551	-5.36	<0.001	***
Asteraceae	(Intercept)	0.856	0.263	3.26	0.001	**
	Pa.inv	1.103	0.335	3.29	0.001	**
	Dry.S	0.234	0.400	0.58	0.559	ns
	Pa.inv x Dry.S	-1.212	0.494	-2.45	0.014	*
Rubiaceae	(Intercept)	1.594	0.572	2.78	0.005	**
	Pa.inv	-0.480	0.483	-0.99	0.321	ns
	Dry.S	-0.102	0.632	-0.16	0.871	ns
	Pa.inv x Dry.S	-0.447	0.710	-0.63	0.529	ns

(c)

Origin	Variable	Factor	Estimate	SE	z	P	Significance
Exotic	**Melinis minutiflora*	(Intercept)	-0.058	0.438	-0.13	0.895	ns
		Pa.inv	1.230	0.512	2.40	0.016	*
		Dry.S	2.446	0.537	4.55	<0.001	***
		Pa.inv x Dry.S	-4.518	0.749	-6.03	<0.001	***
	**Urochloa decumbens*	(Intercept)	-1.216	0.506	-2.40	0.016	*
		Pa.inv	1.958	0.625	3.13	0.002	**
		Dry.S	-1.086	0.841	-1.29	0.197	ns
		Pa.inv x Dry.S	-1.265	1.062	-1.19	0.233	ns
Native	*Baccaris linearifolia*	(Intercept)	0.170	0.413	0.41	0.680	ns
		Pa.inv	1.605	0.549	2.93	0.003	**
		Dry.S	0.773	0.555	1,39	0.164	ns
		Pa.inv x Dry.S	-1.957	0.762	-2,37	0.018	*
	Leandra aurea	(Intercept)	1,080	0.357	3,03	0,002	**
		Pa.inv	-1,168	0.351	-3,33	<0,001	***
		Dry.S	0.274	0.325	0.84	0.398	ns
		Pa.inv x Dry.S	0.611	0.464	1.31	0.188	ns
	Tibouchina stenocarpa	(Intercept)	1,063	0.346	3,07	0.002	**
		Pa.inv	-0.611	0.413	-1.48	0.139	ns
		Dry.S	-1.372	1,012	-1.36	0.175	ns
		Pa.inv x Dry.S	1.523	0.593	2.57	0.010	*

Table 3 – Results of the linear models of the relationship between seed bank structure and biomass production related variables in Cerrado sites invaded by *Ptedium arachnoideum* in southeast of Brazil. Dependent variables are the overall abundance and richness of the seed bank, as well as the abundance of the most common families and exotic species, and independent variables are the litter biomass from *P. arachnoideum* e other species. These models had the lower Bayesian Information Criterion (BIC) values compared to models including biomass and density of *P. arachnoideum*. Significance: *p<0.05, **p<0,01, ***p<0.001.

Model components	intercept			*P. arachnoideum* litter			other species litter			r^2adj	BIC
Variables	SE	t	p	SE	t	p	SE	t	p		
Total abundance	12.72	1.39	0.177	0.02	0.51	0.615	0.05	2.25	0.033*	0.11	260.4
Melastomataceae	8.10	0.26	0.798	0.01	0.82	0.418	0.03	0.48	0.636	0.04	234.2
Poaceae	4.29	2.23	0.035*	0.01	2.48	0.020***	0.02	3.79	<0.001***	0.41	197.3
Asteraceae	6.53	0.90	0.377	0.01	0.55	0.590	0.03	2.06	0.049*	0.09	221.7
Rubiaceae	2.46	1.00	0.328	0.00	1.05	0.305	0.01	2.18	0.038*	0.13	165.1
M. minutiflora	3.23	2.04	0.051	0.00	2.37	0.026*	0.01	3.08	0.005**	0.33	180.9
U. decumbens	2.19	0.63	0.536	0.00	1.02	0.318	0.01	3.33	0.003**	0.28	158.4
Richness	1.57	3.60	0.001***	0.00	0.05	0.964	0.01	0.24	0.810	0.07	139.0

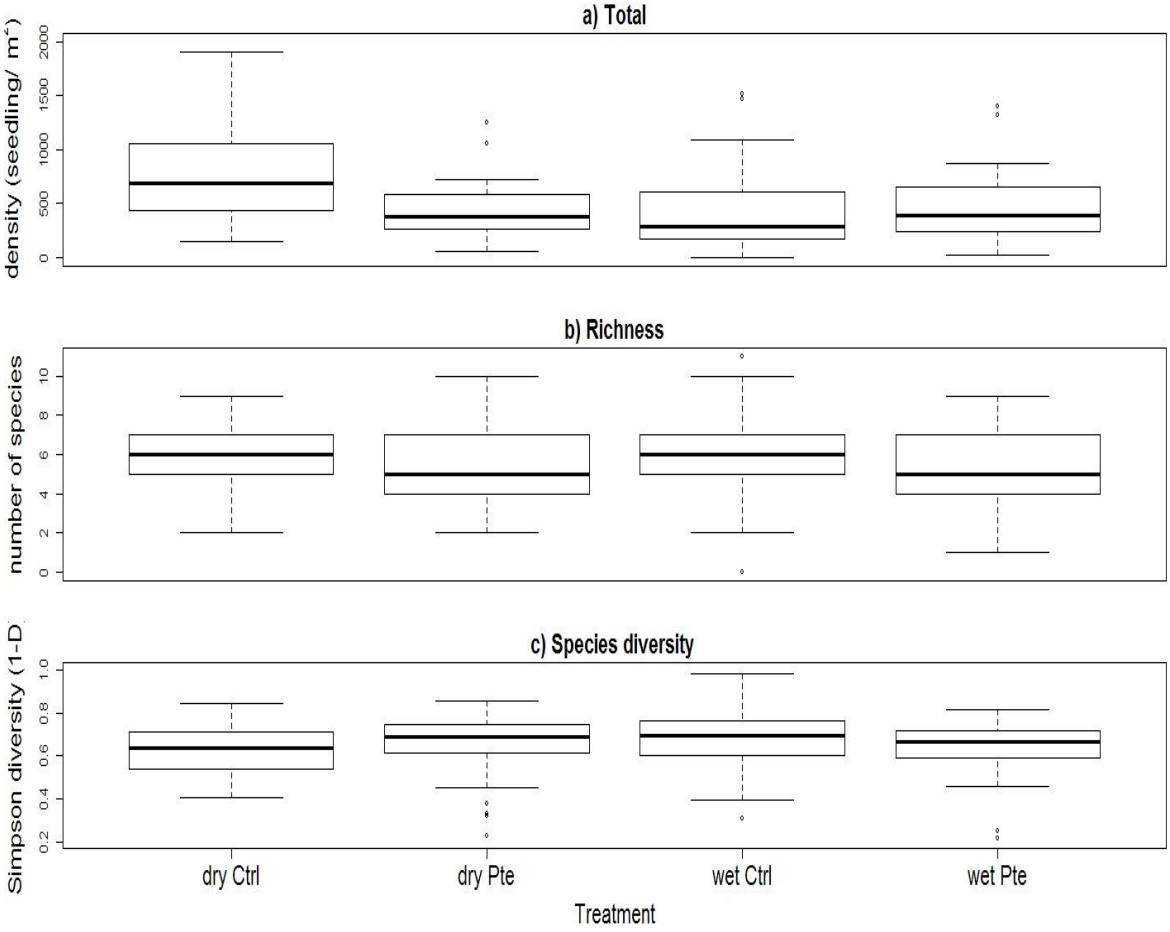

Figure 1. Boxplots of variables related to seed bank structure in sites of Cerrado invaded by *Pteridium arachnoideum* compared with reference uninvaded areas in two different seasons. a) Total seed densities, b) richness, c) Simpson diversity (1-D). Output from generalized linear mixed-effects models (Table 1) is presented. Pte- invaded sites. Ctrl- control sites. Wet- rainy season. Dry- dry season. Significance to comparison between uninvaded and invaded sites on each season: *P<0.05, **P<0.01, ***P<0.001.

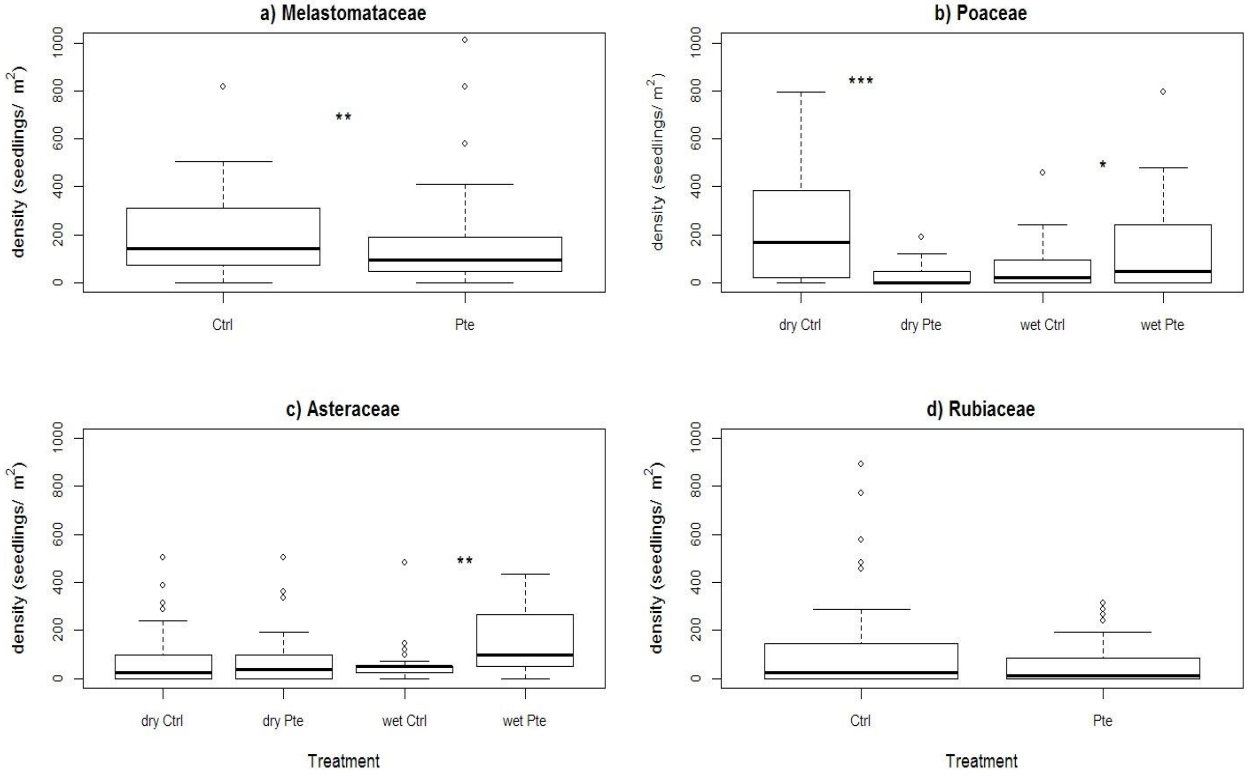

Figure 2. Density of the five commonest families in the seed bank of sites of Cerrado invaded by *Pteridium arachnoideum*, compared to uninvaded adjacent sites. Data are showed both to the rainy and dry season. Output from generalized linear mixed-effects models runned to each family (Table 1) is presented. Pte- invaded sites. Ctrl- control sites. Wet-rainy season. Dry-dry season. Significance to comparison between uninvaded and invaded sites on each season, or between invaded and uninvaded sites when the interaction between season and invasion was not significant: *P<0.05, **P<0.01, ***P<0.001.

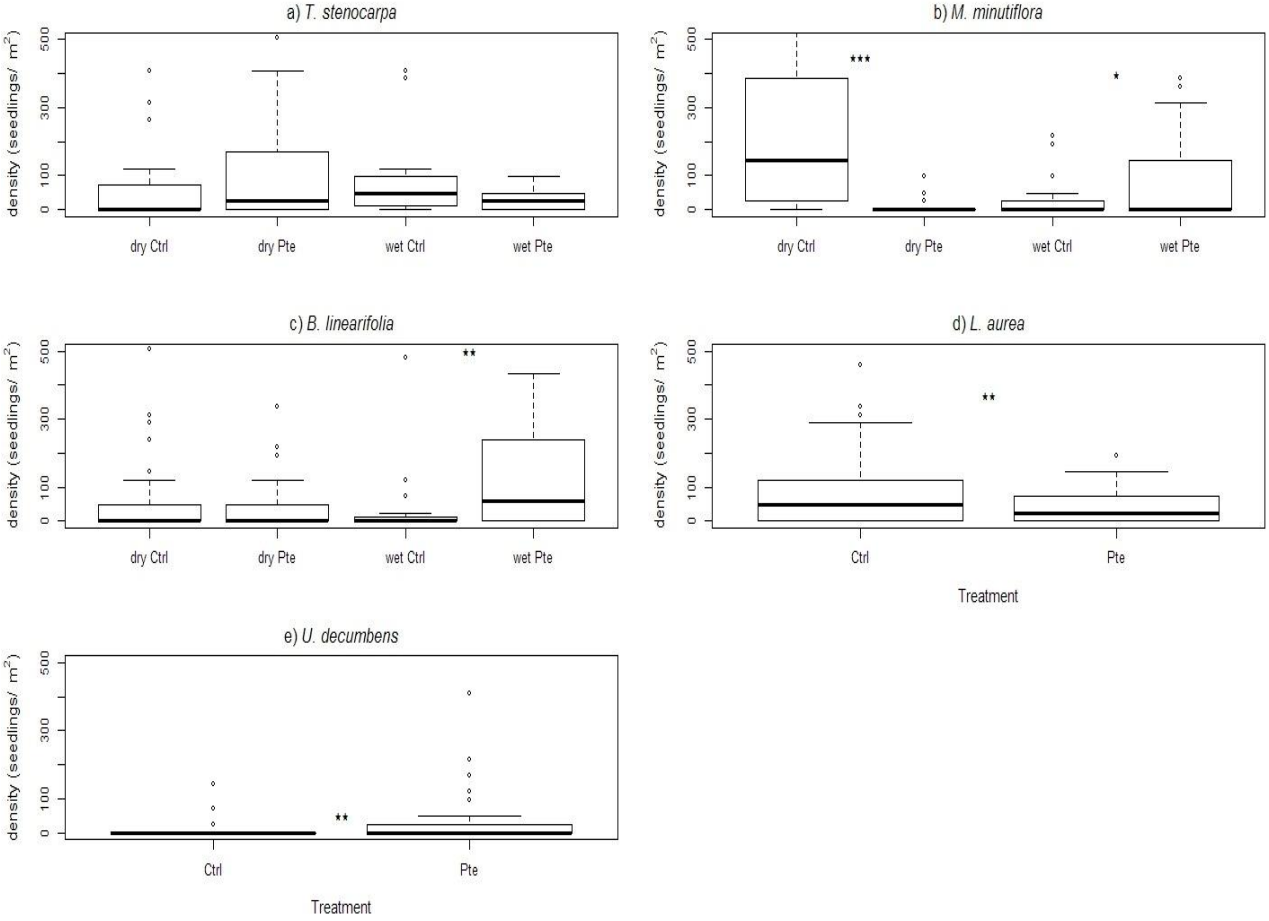

Figure 3. Density of the most common exotic (a-b) and native species (c-e) in the seed bank of sites of Cerrado invaded by *Pteridium arachnoideum*, compared to uninvaded adjacent sites in two different seasons. Output from generalized linear mixed-effects models runned to each species (Table 1) is presented. Pte- invaded sites. Ctrl- control sites. Wet-rainy season. Dry- dry season. Significance to comparison between uninvaded and invaded sites on each season, or between invaded and uninvaded sites when the interaction between season and invasion was not significant: *P<0.05, **P<0.01, ***P<0.001.